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THE PLACENTATION OF THE MANATEE

(Trichechus latirostris)

BY
GEORGE B. WISLOCKI

WITH SEVEN PLATES

CAMBRIDGE, U. S. A.
Printed for the Museum
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INTRODUCTORY REMARKS

Less is known about the placentation of the Sirenia than of any group of mammals. Only two papers, now some fifty years old, exist to the writer's knowledge, regarding this subject. These, by Harting (1878) and Turner (1889), describe the nature of the fetal membranes in two rather poorly preserved specimens of *Halicore dugong*. Consequently it was of considerable interest to me to receive a well-preserved, intact uterus and fetus of the Florida manatee (*Trichechus latirostris*). Study of this specimen revises and extends to a large degree the previous knowledge of placentation in the order Sirenia. A brief summary of the salient features of the placentation of the manatee, as observed in this specimen, has been recently published (Wislocki, 1933).[1] I wish to express my deep gratitude to Mr. George Nelson of the Museum of Comparative Zoölogy of Harvard University for securing this valuable and well-preserved pregnant uterus.

GROSS DESCRIPTION

The specimen consists of an entire gravid uterus containing an excellently preserved fetus *in situ*. The length of the fetus is 44 cm. from snout to tip of tail. The fetus, which is a male, possesses the well-developed outer form of a manatee. The skin at this stage is set with scattered short hairs or bristles. The outer character of the fetus is well depicted in figure 1.

The uterus is a bilobed object consisting of two short, stout cornua, one of which, containing the fetus, is very much enlarged. The ovaries had been removed from the specimen; the Fallopian tubes and cervix are present. The relationships of the uterus to the fetus and the fetal adnexa are shown semidiagrammatically in figure 1. The fetus and its membranes including the placenta are located entirely in the right horn of the uterus, no opportunity being given, by virtue of the narrowness of the uterine lumen in the lowermost uterine segment, as well as by the fact that the two cornua join almost at the cervix, for the fetal membranes to extend into the opposite horn.

The most striking thing upon opening the uterus is the appearance of the placenta. It surrounds the fetus as a thick, sharply delimited purple belt or gir-

[1] In this note I designated my specimen of the Florida manatee as *Manatus latirostris*, basing my terminology upon the classification given in the second edition of Max Weber's well-known book. I have now changed the designation to *Trichechus latirostris*, following the advice of Dr. Glover M. Allen.

dle of the typical zonary type. Its appearance can in no sense be construed as being diffuse. Its gross topography and relationships are presented in figures 1, 2, 3 and 5.

The umbilical cord is a relatively short, stout mass which radiates like a collapsed tent from the umbilical ring towards the placenta. The umbilical vessels, of which there are two arteries and one vein at the umbilicus, divide, within a centimeter or two from the ring, into four sets of paired vessels which proceed as four pedicles towards the placenta upon reaching which they undergo further divisions. The nature of these leashes of diverging vessels which constitute the umbilical cord is shown in figure 2. In addition to the four major sets of paired vessels, one seemingly aberrant vessel, a small artery, is given off singly and proceeds, unlike the others, around the whole circumference of the amnion to reach the placenta at a place remote from the umbilical cord (figs. 1 and 2).

The placenta constitutes a broad girdle or zone of sharply defined tissue which is placed to one side of the equator of the entire blastocyst, so that one membranous chorionic pole is more extensive than the other (figs. 1 and 2). The smaller pole is oriented towards the uterine outlet. Both chorionic poles are completely membranous. The placenta is grossly of the type described as zonary and is made up of a series of rather intimately cemented lobes of variable size and contour ranging from four to eight centimeters in diameters (figs. 2 and 3). The tendency to form lobes is best discerned along the periphery of the placenta. On cross section the placenta is found to consist of a rather firm plate of tissue, about one centimeter in thickness (fig. 5). The outer half of the placenta is deep red or purple, whereas the basal half, constituting its zone of junction with the endometrium, is whitish, containing the cut aspects of numerous endometrial arteries and veins. The border of the placenta is elevated, possessing a smooth contour and a slightly undercut edge (fig. 5). From this border the chorion leaves the placenta as a stout, whitish membrane. In the placental zone the fetal tissues cannot be stripped off from the maternal, because the interlocking of the two is much too intimate. Outside the area of the zonary placenta the chorion separates easily from the uterus, its outer surface presenting the appearance of a smooth membrane. The uterine surface which is uncovered by stripping away the chorion, is almost identically smooth. There are, however, scattered near the placental border some half dozen small, round areas no larger than a half of a centimeter in width where the chorion clings tenaciously to the endometrium. These minute discoidal patches are reddish. On microscopic section they prove to be, as their gross appearance suggests, minute areas of chorionic attachment structurally resembling the placenta. They are true accessory placental areolae, but their

total area is quite negligible, and accordingly their functional significance must be practically nil. The gross appearance of these areolae is shown in figures 2, 3 and 6.

The fetal surface of the membranous chorion is fused throughout its entire extent with the allantois. This chorio-allantoic membrane is supplied by abundant blood-vessels, readily visible to the naked eye, which are derived from the placental vessels (fig. 2).

The relationships of amnion and allantois are complex. They are shown semidiagrammatically in figures 1 and 2. The allantois is a lobulated sac which is extensive, and is fused everywhere with the chorion from pole to pole, excepting for a small triangular area (figs. 1 and 2) where the amnion succeeds in applying itself to the chorion. Thus the allantoic sac is much more extensive than the amniotic sac, and surrounds it with the exception of the small triangular area of amnio-chorionic fusion.

The allantois consists essentially of four saccular diverticula, two small median and two larger lateral ones. These sacculations are related to the curious umbilical pedicle. The latter, as has been said above, consists of four stout diverging pairs of blood-vessels which can be likened approximately to the four edges of a hollow quadrilateral pyramid. The space within the pyramid is a common allantoic antrum from which commodious sacculations lead off through the four sides of the pyramid between the marginal leashes of blood-vessels. An attempt to show these complicated relationships has been made in figure 2. The membranous walls of the bulging sacculations form mesenteries of reduplicated allantois, which ensheath the respective leashes of blood-vessels and give them a mesentery-like attachment along their outer borders. The two major sacculations extend into the poles of the chorion, fusing with the latter and completely enclosing the amnion. The two lesser sacculations occupy the equator of the chorionic sac, lying side by side, and fused with the chorion of the placental surface. It is distal to the apices of these two sacculations that the triangular area not occupied by the allantois exists where the amnion achieves a restricted fusion with the chorion overlying the placenta (fig. 2). It will be noted that this area of amnio-chorionic fusion is triangular with its base near the umbilicus and its apex on the placenta contiguous to the apices of the two lesser allantoic sacculations. At this point a curious, shallow vortex is formed on the surface of the placenta into which the amnion apparently dips (figs. 1 and 2).

The blood-vessels supplying the placenta and fetal membranes merit a brief description. The vessels at the umbilical ring are three in number: two arteries

and one vein. About two centimeters from the umbilical ring these divide giving rise to four sets of divergent paired vessels which proceed to the surface of the placenta. In addition to these a peculiar artery of medium size, without accompanying vein, branches off from one of the umbilical arteries and courses between the amnion and allantois to a distant point on the opposite side of the placenta (*art.*, figs. 1 and 2). Moreover, a number of minute blood-vessels are given off at irregular intervals from the above enumerated paired vessels, which supply the walls of the amniotic and allantoic sacs with a few fine branches. Thus the membranous walls of these sacs are not totally devoid of blood supply. Upon approaching the surface of the placenta the four major pairs of vessels constituting the umbilical pedicle give off large branches which pass to the adjacent placental surface (fig. 3). The main stems of the original vessels, however, upon reaching the surface of the placenta, course for long distances diminishing ultimately in size by giving off numerous subsidiary vessels. These subsidiary branches, while traversing the surfaces of the placental lobes, give off a multitude of finer branches (the ultimate ones visible to the naked eye) which run from the centrally placed vessels to the periphery of the lobes, lending to the surface of the latter a finely streaked appearance (fig. 3).

At the periphery of the zonary placenta numerous medium-sized and small arteries and veins enter the membranous chorion supplying it to its utmost poles with an abundance of small vessels (fig. 2). Thus the membranous chorio-allantois is amply vascularized. The vascularity of the membranous chorio-allantois is much greater than that of the amnio-allantois or of the membranous reduplications of allantois covering the leashes of umbilical vessels. The latter are relatively vascular in the neighborhood of the umbilical cord, but become less so as one leaves the vicinity of the large vessels. Areas of amnio-chorion are encountered, as one retreats from the vicinity of the cord, in which the slender vessels supplying them appear to have become occluded. This observation suggests that the walls of the amniotic and allantoic sacs are destined at later stages to lose much of their present blood supply.

Nothing has been said yet of the curious morphology of the walls of the placental vessels. The four pairs of vessels constituting the umbilical pedicle reach the placental surface, whereupon they give off branches which extend to all parts of the placenta. These vessels are not buried in the placenta but are raised for the most part from the surface, giving the appearance of being embossed upon it. Some of them are free to the extent of possessing small mesenteries. The most characteristic thing regarding these vessels is the nature of their adventitial

sheaths. These are thickened in a multitude of places to produce a variety of protuberances projecting into the allantoic cavity (figs. 2, 3 and 4). These bodies are white with a waxy lustre. They occur about equally along arteries and veins, but are uneven in number and distribution in different parts of the placenta. Moreover, a small percentage of them protrude from the placental surface without any distinct relationship to recognizable placental vessels. These bodies are of three general types with all transitions between them (fig. 4). The most common is undoubtedly a protuberance on the vessel wall, seemingly like a drop of wax. In a few instances these drops follow one another so closely as to give a beaded appearance. Again for short distances vessels may appear as though they had been coated with wax. Next in order of frequency come protuberances that have surfaces which, instead of being smooth, are cauliflower-like. Finally, in frequency come similar cauliflower-like masses which, instead of resting directly upon the placenta, are attached to the placental surface by short stalks or in some instances by long threads. The cauliflower-like terminal expansions of these pendulous structures are often flattened. None of the structures enumerated are large, their greatest size being two to four millimeters in diameter, although the threads by which the longest pedunculated ones are attached may attain in some instances a length of one to three centimeters. These various appendages are irregularly distributed over the entire surface of the placenta, including that small triangular area to which amnion instead of allantois is attached. They accompany the blood-vessels which leave the placental border to vascularize the membranous chorion for only one to three centimeters at most. Thus the inner surface of the membranous chorio-allantois is practically devoid of them. Moreover, there are but occasional ones on the remaining membranous walls of the allantoic sacculations. Similarly there are none visible to the naked eye on the umbilical cord. The amnion, excepting for a few excrescences limited to that small area of the amnion which is fused with the placenta, is otherwise devoid of these structures. The amnion possesses, nevertheless, a curious texture. Running one's finger over the wall of the amniotic sac gives the sensation of cloth on which fine grains of sand have been sprinkled and on close inspection it can readily be seen that, instead of being smooth, the surface is closely studded with the smallest visible, whitish particles constituting minute elevations from the surface. In contrast to the amnion the interior surface of the allantoic cavity is smooth, like the surface of glass, excepting where its texture in the region of the chorion and placenta is affected by the above described appendages.

MICROSCOPIC DESCRIPTION

The most interesting part of the microscopic examination of this specimen concerns the nature of the zonary placenta. Both of the previous investigators (Harting and Turner) examined the placental area of their alcoholic specimens by rather primitive means, resorting mostly to studying small teased bits or free-hand sections. Their pictures of these preparations show the inadequacy of the technique. However, from their observations they both came to the conclusion that placentation in *Halicore dugong* is diffuse and adeciduate consisting of simple interdigitation of intact fetal and maternal villi. This finding is contrary to the present observations of the Florida manatee. The sections of the present specimen, which are fixed and stained by modern technique, show beyond a doubt that the zonary placenta of the manatee is a highly complex labyrinthine one of deciduate character. That this observation holds also for the closely related dugong is extremely probable in view of the fact that grossly in numerous major particulars, in so far as the accounts of Harting and Turner go, the morphology of the placenta and fetal membranes in our several specimens tallies completely.

Following these anticipatory remarks, I shall pass to a detailed description of the microscopic structure of the placenta in the present specimen. The zonary placenta is a lobulated, thick band varying from one to one and a half centimeters in thickness (fig. 5). It is composed of an irregularly thickened, relatively pale-staining layer of tissue on the fetal surface of the placenta in which the fetal vessels are distributed. Beneath this outer covering is a lamina some four to five millimeters thick constituting the placental labyrinth in which the fetal and maternal circulations become intimately united (fig. 7). This zone stains very deeply. Beneath this is a light-staining zone of about equal thickness composed of maternal tissue upon which the labyrinth rests.

The placental labyrinth upon microscopic examination proves to be completely deciduate in that it is composed of a fine-meshed trellis-work of fused maternal and fetal tissues in which separation of the two is impossible and in which there has been a loss on the maternal part of most of the cellular components of the endometrium (figs. 12, 13, 14 and 15). The fetal capillaries in the labyrinth are recognizable because the blood within them contains here and there nucleated red blood cells. The endothelium lining the capillaries is distinguishable, and accompanying the slightly larger vessels there is an additional sheath of fetal mesenchyma. The fetal capillaries are oriented for the most part in rows from the

surface to the base of the placenta, but there are besides numerous anastomoses between them so that they are to a considerable degree plexiform. The maternal blood spaces are narrow, tortuous channels, for the most part not injected with blood, lying in the meshes between the fetal plexus. In places, however, blood is recognizable within them, distinguishable from that in the fetal capillaries by the relative abundance of leucocytes in it and the absence of nucleated erythrocytes.

Separating the maternal from the fetal vessels are narrow laminae of cells, an interpretation of the nature of which is important in determining the type of placental labyrinth which we have before us. These cells appear to be all of the same character and to be syncytial in that boundaries between them are not visible. They have large, oval nuclei surrounded by a relatively abundant, rather pale-staining cytoplasm. These syncytial sheets of cells invest the walls of the fetal capillaries. They enclose on their opposite faces the maternal capillaries and constitute in my estimation the limiting walls of the maternal blood channels. If this interpretation be correct, the syncytium in question is trophoblastic and of fetal origin. It constitutes, moreover, the sole enclosure for the maternal blood, the latter circulating in labyrinthine spaces lined by trophoblast. Evidently, then, the maternal blood-vessels must have lost all of their tunics including the endothelium, making of the labyrinth a hemochorial one according to the concept of Grosser. This decision has not been simple to make, because of the complexity of the tenuous layer of cells between the two circulations. The possibility remains that the syncytium intervening between the two circulations may not be uniform in character or derivation, and that some of the homogeneous cells making up the lamina may be swollen and altered maternal endothelium. However, after much study of the sections I believe that the interpretation that there is a hemochorial type of labyrinth before us appears to be justified. The alternative permitted would be that it is in whole or part an endotheliochorial labyrinth. Study of other specimens of the placenta when further stages are obtainable may give a more complete answer to this question. There remains, however, absolutely no doubt whatsoever about the essential fact that the labyrinth is truly deciduate, the endometrium having been invaded by trophoblast with the complete destruction of the maternal epithelium and connective tissue with the ultimate intimate fusion of the trophoblast with eroded maternal blood channels. These findings are, moreover, fully substantiated by studying the peculiar morphology of the surface as well as the base of the placenta.

At the base of the placenta tongue-like masses of fetal tissue, resembling

chorionic villi, can be seen penetrating the mucosa (figs. 15, 17, 18 and 21). The latter is undergoing wide-spread erosion in the neighborhood of the advancing trophoblast. These processes of fetal tissue are covered externally by trophoblast; in their interior they contain cores of vascularized fetal mesoderm. Unlike the trophoblast of the placental labyrinth which is syncytial and pale staining, the trophoblast covering the growing tips of the villous processes, which are invading the mucosa, is composed of cells which are small, with deeply staining nuclei, and which are for the most part rather regularly set. Indeed in many places the cells appear to constitute cytotrophoblast instead of being syncytial. Between the tongues of the chorionic villi are narrow bands of pale, rather acellular, degenerating maternal connective tissue. At intervals where large maternal blood vessels reach the neighborhood of the placenta, the chorionic villi have penetrated more actively into the mucosa, sending out long sprouts which exhibit a tendency to follow the walls of the blood-vessels and to ensheath them (figs. 17, 18 and 21). A curious observation is that the trophoblast on the side of the chorionic process applied to the maternal vessel changes its character completely. The darkly staining trophoblast composed of small cells, which is characteristic of these basal prolongations of the chorion, changes where it comes in contact with the wall of the maternal vessel into syncytial trophoblast whereby the trophoblastic cells immediately become paler in staining reactions of both cytoplasm and nuclei (figs. 17, 19 and 21). This enclosing of the maternal vessels is accompanied by degeneration of the two outermost vascular tunics, adventitia and media, so that the maternal blood comes to flow in a confining channel of trophoblast. To what extent the endothelial elements of the maternal vessel remain intact within this sheath is difficult to say with absolute certainty. In some vessels the endothelium can be seen definitely as a thin, nuclear membrane (fig. 17), but in other vessels, in places along their walls, it is not discernible (figs. 19 and 21). The endothelium being exceedingly delicate, coupled with the fact that the specimen, although well fixed, may not have been perfectly fixed for the complete preservation of so delicate a membrane, leads me to presume that it was completely present during life in these larger afferent and efferent maternal trunks.

The uterine glands play no conspicuous rôle in the formation of the placenta. Some distance below the basal layer of the labyrinth, in a less compact zone of the mucosa, there are groups of glands scattered at irregular intervals (fig. 16). These glands are conspicuous neither by virtue of size nor by evidence of being markedly secreting. They are small, with walls composed of a single layer of

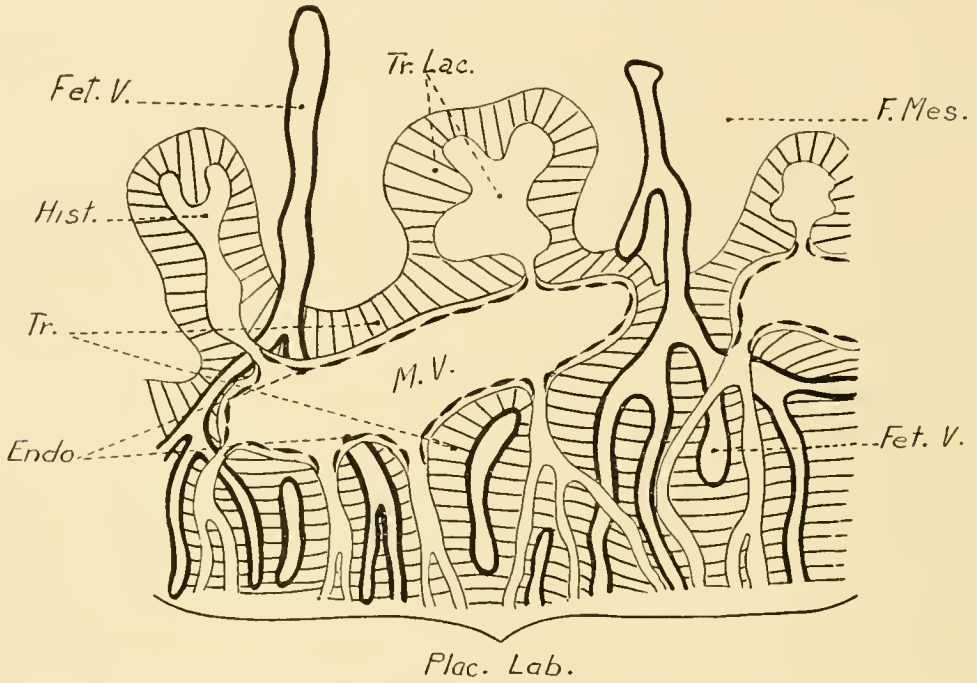
low cells which are not unusually active. Their ducts pass outward toward the base of the placenta where they are evidently sealed off. Rarely, one of the glands in close proximity to the placental base appears to be somewhat dilated, and in one section I have come across a place where the trophoblast has erupted into the lumen of such a dilated gland (fig. 20).

Passing from a description of the basal portion of the placenta, it is necessary to turn our attention to the fetal surface of the organ (figs. 12, 22 and 23). Here some rather extraordinary features are present. The larger afferent maternal vessels, endothelial-lined but otherwise ensheathed by a tunic of trophoblast, penetrate the placenta to reach the fetal surface of the labyrinth (fig. 22). In this external zone of the labyrinth the vessels divide into short branches many of which run parallel to the surface (fig. 23). These possess, in that side of their wall adjacent to the labyrinth, numerous openings leading into the ultimate intervillous or intertrabecular spaces of the fine-meshed labyrinth. It is at these transition points from larger afferent vessels to the labyrinthine capillaries or sinusoids that the maternal endothelium is lost, the maternal blood from this moment on circulating in the interstices of the labyrinthine trophoblast. The opposite sides of the vessels bear a curious relationship to the trophoblast at the surface of the placenta. Between these vessels and the limiting trophoblast at the surface of the labyrinth is a series of recesses or lacunae containing stagnant maternal blood which is being actively phagocytized by trophoblastic cells (figs. 12 and 22). These recesses containing extravasated maternal blood constitute a narrow zone covering the entire placenta. Thus provision is made in this region for histiotrophic nourishment of the fetus by the destruction and assimilation of stagnated maternal blood. This formation is the equivalent of the hematomata (green and brown borders of carnivores) and other devices, mostly paraplacental structures, for the histiotrophic nourishment of mammalian fetuses.

In order that my readers may understand more fully the nature of the structures which I am attempting to describe, I have constructed a diagram (text-fig. 1) giving my interpretation of the morphology of the zone under discussion, besides a number of photographs of the actual histological sections (figs. 12, 22 and 23).

It is evident beyond doubt from the sections that there is a series of small trophoblastic lacunae over the whole surface of the placenta. These pockets contain stagnated maternal blood. The trophoblastic cells lining the pockets are unlike the trophoblastic cells seen in the form of syncytium in the bulk of the placental labyrinth or as small-celled cytotropho-blast described at the growing base

of the placenta. The trophoblastic cells in these recesses are separate, discreet, broad columnar cells with somewhat basally situated nuclei and a large amount of distally placed vacuolated cytoplasm. In the cytoplasm are large numbers of whole or fragmented erythrocytes, as well as a quantity of golden pigment, the latter usually in the neighborhood of the nucleus.



Text-fig. 1. Diagram illustrating the author's interpretation of the structure and nature of the surface of the placental labyrinth in the manatee. *F. mes.*, Fetal mesoderm clothing the surface of the placenta and accompanying the fetal vessels entering the labyrinth. *Fet. v.*, Fetal vessels entering the labyrinth. *M. v.*, Maternal vessel lined by endothelium (*Endo.*) communicating above with trophoblastic lacunae (*Tr. lac.*) which contain stagnant maternal blood (*Hist.*) undergoing absorption by the trophoblast; and below by a series of openings into the maternal blood channels of the placental labyrinth (*Plac. lab.*). Note that neither the lacunae on the one side of the maternal vessel nor the channels leading into the labyrinth on the opposite side are lined by endothelium.

The question arises as to how these extravasations of maternal blood occur. Their source is to be sought in the subjacent afferent maternal vessels which are lined by endothelium ensheathed in trophoblast. The endothelial walls of these apparently give way in places, allowing maternal blood to escape through the endothelium into adjacent pockets of trophoblast in which no free circulation is possible, so that stagnation follows.

One could conceive that such an extravasation, once having escaped the limits of the maternal vessel might by its mere pressure lead to the formation of a pocket-like indentation of the surrounding trophoblast. This may be sufficient reasoning to explain matters. However, I offer a further suggestion from a clue

given by examination of the extreme border of the placenta. Here, as one approaches the edge of the placenta, the blood-containing lacunae dwindle in size and amount of contained blood (fig. 23). The pockets are finally replaced on the ultimate placental margin by clusters of syncytial trophoblast with vacuolated, degenerating centers. Thus the precursor of the lacunae appears in all likelihood to be a mass of redundant trophoblastic syncytium which has accumulated between the maternal vessels and the overlying fetal stroma of the chorio-allantois. The cores of these trophoblastic accumulations undergo vacuolar degeneration, whereby the wall of an adjacent maternal vessel becomes weakened, so that maternal blood extravasates into the degenerated core of the adjacent trophoblast. Rearrangement of the cells takes place in the structure, eventuating in the trophoblast becoming columnar and actively phagocytic. Moreover in the course of time the pockets, initially small, become considerably larger. This is a reasonable explanation, I believe, of the formation of the pockets and follows logically from the observations. Naturally the relationships in this zone are complex, and it will doubtlessly require study of further stages to elucidate the problem fully.

Leaving the placenta proper, I shall pass to the description of several other important structures. The allantois, and more particularly the excrescences seen grossly on its walls, arouse curiosity as to their nature. The allantois is lined throughout by a single layer of small epithelial cells. Without any seeming regularity these may be flat and button-like, or, on the other hand, for a certain distance the cells may be elevated like small clubs, with the small dark-stained nucleus at the attached end, and a large vacuole at the clubbed, distal end (fig. 27). Nowhere, where sections have been taken, is there any evidence of layering of the epithelial cells.

The waxy excrescences, so numerous along the walls of the allantoic vessels supplying the placenta, are found on microscopic examination to be due merely to a proliferative growth of the mesodermal stroma of the allantois. The minute character of these structures is shown in figs. 25 and 26. The main difference between them and the ordinary mesodermal tissue, seen elsewhere in the fetal membranes, lies in the facts that the tissue has a more easily perceived interlacing fibrillar matrix, that the cells are fewer, and that the cell outlines are more irregular than ordinary, resembling mesenchymal cells as seen in rapidly growing embryonic tissue or tissue cultures. These proliferative growths, as well as the remaining bulk of the chorio-allantoic connective tissues, are supplied with minute blood vessels.

Leaving the allantois, I shall pass to a few descriptive remarks concerning the paraplacental border and uterine mucosa. At its border the placenta tapers down to a wedge, without changing its character to any extent, and disappears (figs. 5 and 8). From its edge arises a thick sheet, the membranous chorion. Fused with the allantois by a heavy sheet of well-vascularized connective tissue, the latter presents on its uterine surface a palisade of columnar cells with basally situated nuclei (fig. 24). The chorion is not fused with the uterine mucosa. The latter, a millimeter from the border of the placenta, shows the character of a completely intact mucous surface provided with a complete epithelial covering (figs. 8 and 11). The uterine epithelium is composed of slender, high, columnar cells closely packed. It is worth noting that minute, endo-epithelial cysts occur at short intervals in the uterine epithelium. These are small vesicular structures, as a rule no thicker than the epithelium itself, filled with secretion and with walls composed of modified columnar cells which have become flattened out around the lumen of the vesicle (fig. 11). These structures have a configuration of their walls, resembling strikingly the figures of so-called endo-epithelial glands, but in no instance in my sections have I seen them open onto the surface, so that I interpret them as being cystic instead of glandular.

Beneath the uterine epithelium is a narrow layer of loose stroma which reaches down to the musculature. In this layer one encounters at intervals small nests of uterine glands, simple in architecture, with small, low epithelial cells lining them and presenting no evidence of marked activity (fig. 16).

Near the placental margin, as described in the gross description, there are about a dozen minute, scattered areas, some two to four millimeters in diameter, in which chorion and uterine epithelium are fused, leading to the formation of minute, accessory, placental areas. A photograph of a section through one of these accessory placental areolae is shown in figure 10.

The umbilical cord on low power examination, about two centimeters from the umbilical ring, shows three blood vessels: — two arteries and a vein, besides an extensive cleft, the allantoic duct (fig. 9). Grossly the surface of the umbilical cord appears smooth without apparent carunculae. On section, however, one encounters scattered patches of thickened umbilical (amniotic) epithelium. The section is taken from the short cord about one and one-half centimeters distant from the point, within a few millimeters of the umbilical ring, where the black, pigmented skin of the fetus gives way to the white, unpigmented tissue of the cord. Another observation of some interest is that the connective tissue stroma of the cord is well vascularized by small arterial and venous branches of the

umbilical arteries and veins. The stroma thus has a plentiful capillary blood supply. Noteworthy is the fact that in some areas the venulea are almost cavernous in character. The presence of vascularized stroma in the umbilical cord of mammals is rather the rule than the exception, as I have discussed in a recent paper on the placentation of the porpoise (Wislocki, 1933). With the exception of the Primates, I have found the stroma of the umbilical cords of the majority of mammals well vascularized during the whole course of gestation. This vascularization cannot be attributed solely, as explained there, to the presence of persistent vitelline vessels. In the present specimen, for example, no trace of a vitelline duct or vessels can be found in sections of the umbilical cord.

The minute elevations discovered in the gross upon the surface of the amnion prove upon section to be composed of a delicate core of stroma clothed by epithelial cells. The latter differ from the ordinary epithelium covering the amnion in that they are larger and sometimes vacuolated. I have noted in some of these minute appendages cystic transformation of the epithelium, as well as degenerative changes involving both epithelium and stroma. The usual character of one of the appendages is shown in figure 28.

THE CERVIX AND VAGINA

A brief description is appended of the cervix and its relationships because of the rarity of the present material. The external genitalia do not accompany the specimen.

The lumens of the right and left uterine cornua unite as shown in figure 1 to form a relatively short, common, uterine cavity. The latter, which is approximately nine centimeters long, terminates at what I judge to be the cervical outlet. The lumen of the uterine body, as well as of the cornua, is circular with the mucosa thrown into low, longitudinal folds. What is presumed to be the uterine outlet is a dense, rubbery mass perforated in the center by the transversely flattened canal of the cervix (fig. 1a). This mass, about eight centimeters in diameter, protrudes quite definitely into the cavity of the vagina running at almost right angles to it. The protruding cervix is cleft by deep furrows radiating from the cervical outlet. Its margin is delineated by a circular furrow, caudally much undercut, so as to constitute a deep fornix.

The cavity into which the cervix protrudes lies at right angles to it and is flattened anteroposteriorly. Its lateral margins have the outline of a pear, the bulbous part surrounding the cervix, the constricted portion extending toward the

genital vestibule. The walls of the vagina are composed of a number of heavy, rubbery folds of mucosa which converge toward the somewhat constricted vaginal outlet. This vaginal segment is about twelve centimeters long. The bladder wall, partly intact, attaches to the ventral surface of the lower uterine segment, and the urethra leaves the neck of the bladder to join the genital passage at the point where the specimen has been amputated. The point of junction of the urethra with the genitalia passage is well external to the cervical orifice, making it plausible to assume that the recess into which the cervix opens is homologous to the vagina of other mammals, the urogenital sinus or vestibule being in that case the outlet beyond and external to the urethral meatus. I give this brief description of the topography of my specimen because the interpretation of the presence of a vaginal segment differs from the observations by Freund (1930) of a virginal uterus in which cervix and urethra opened so close together that the recess which formed a common outlet for them was interpreted as the vestibule, so that a vagina seemed to be totally lacking. I present my observations merely to call attention to the need of examination of other specimens.

DISCUSSION

The present observations upon the placenta of the manatee place the placentation of the Sirenia in an entirely new light. The only previous accounts of placentation in this order of mammals are by Harting (1878) and Turner (1889), each of whom described a fetus and placenta of the dugong. Their rather brief accounts of the gross topography of the fetal membranes in the dugong bear a striking resemblance to the gross findings in the present specimen of the manatee. Thus the configuration and relationships of allantois and amnion are in the main about the same. The curious structure of the umbilical cord coincides in both genera. The placenta in Turner's specimen (length of fetus, 163 cm.) is zonary as in the manatee, whereas in Harting's much younger specimen (length of fetus, 27.8 cm.) the placenta is quite diffuse, excepting bare spots at the chorionic poles. This dissimilarity between the two dugongs Turner ascribes to the differing ages of the specimens, with which I agree. In my own specimen of manatee, in which the fetus is considerably longer than Harting's, the placenta is completely zonary coinciding with Turner's specimen. Thus grossly the placental topography of the manatee and dugong is manifestly alike.

When it comes to the microscopic examination of the placenta, however, our findings diverge radically. Careful examination of my specimen reveals it to be

a deciduate, hemochorial placenta of marked complexity. Harting's and Turner's dugong placentae, on the other hand, are described as consisting of an interlocking of intact fetal and maternal villi in the manner characteristic of the ungulates and designated as diffuse. Against their findings are the facts that their examinations were carried out on crude histological preparations (free-hand sections and teased preparations) and their material was poorly preserved for microscopic work. In view of the great similarity of our several specimens upon gross examination, I am inclined to believe that microscopically the placentae will be found in the main to be identical as soon as modern histological technique is applied to a placenta of the dugong. From careful consideration of the matter, I am forced to the conclusion that placentation in the manatee, and in all likelihood in the Sirenia in general, is deciduate and hemochorial.

These findings necessitate a reconsideration of the place of the Sirenia in placental classification. In this regard the Sirenia must be removed from the Ungulata and Cetacea with their totally different placentation.

If this is the case, to what groups of mammals do the Sirenia bear placental affinities? The placenta being zonary and deciduate naturally invites comparison with other zonary and deciduate placentae: the carnivores, Hyrax and the elephant. Aside from its zonary shape, which is of no great importance in deciding placental affinities, the placenta of the manatee bears no great structural affinities to the dog or cat. The placentae of the latter are endotheliochorial; they have characteristically specialized placental borders, and the endometrium exhibits during the first part of gestation a characteristic profuse glandular reaction. None of these features of the carnivores is present or marked in the manatee. Aside from the external form, the two types of placentae are dissimilar.

With the two other groups of mammals, the Hyracoidea and the Proboscidea, whose placentae are zonary and deciduate, the resemblances are more far-reaching. The placenta of Hyrax has been the subject of study in recent years by Assheton (1906), D. Thursby-Pelham (1924), and Wislocki (1930). On comparing their accounts of the placentation of the hyracoids with the present description of the placenta of the manatee, one is struck by the great similarity in the major characteristics. The placenta of Hyrax is grossly in the beginning almost diffuse, becoming later distinctly zonular. The labyrinth is, moreover, hemochorial, differing therein from the zonular placenta of the carnivores. The amnion is surrounded completely by the allantois which is voluminous. The umbilical cord branches into four pedicles of paired blood-vessels which reach the placenta. These pedicles constitute the limiting borders of four sac-like

dilatations of the allantois, according to Assheton and Thursby-Pelham, two of which occupy the poles of the blastocyst, while two smaller sacculations are apposed to the surface of the zonary placenta. The striking similarity in many major points between the placentation of the manatee and the hyracoids is apparent. It may be stated with certainty that the resemblance is greater than to any other known form, unless it be the elephant.

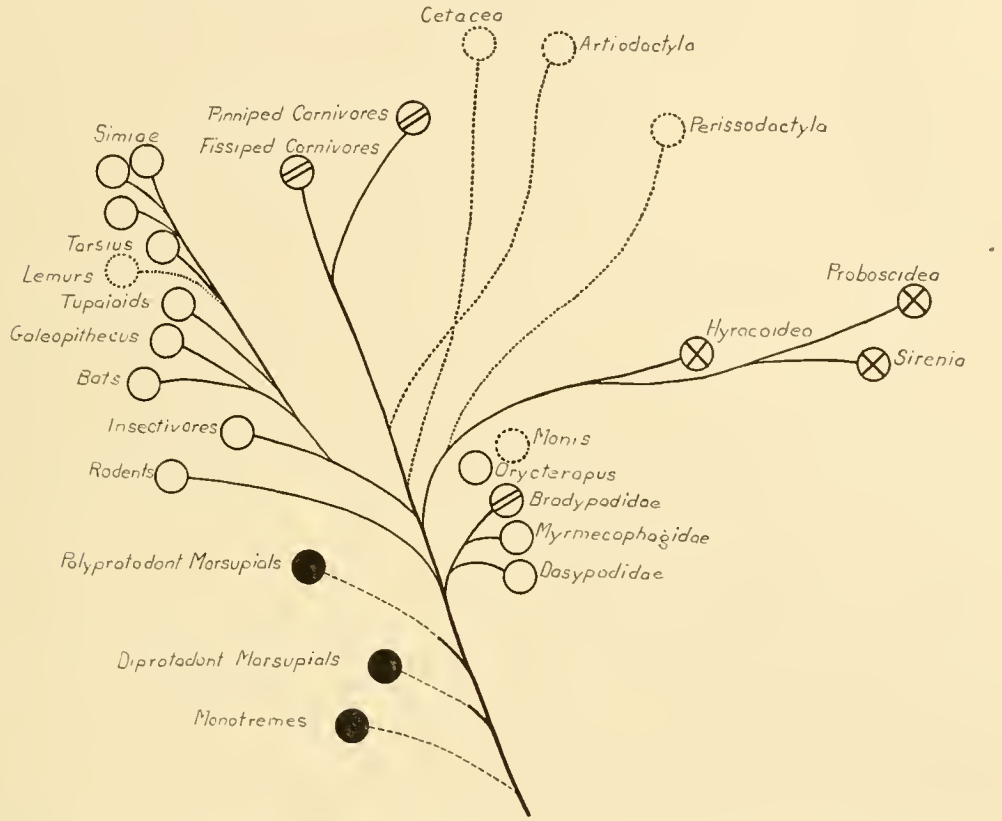
The placentation of the elephant is very incompletely known, even for a single stage. However, on reading over the papers by Owen (1857), Chapman (1881, 1899), Assheton and Stevens (1905), Assheton (1906), and Boecker (1907), it is apparent that the placenta is zonary and deciduate. The gross topography of the placenta and membranes is sufficiently clear in the text and illustrations in the papers by Owen (1857) and Chapman (1881) to acquaint one with the major characteristics of its placentation. On studying their accounts and figures, I am impressed by the striking resemblances between the placenta in the elephant and in the manatee. The shape of the chorion, the character of the zonary placenta, the division of the umbilical cord into four sets of paired vessels, the extensive allantois which is sacculated and surrounds the amnion, the presence of allantoic bodies attached to the placental vessels all contribute to making the resemblances very striking. On the basis of the gross configuration of the placenta and membranes, the manatee, Hyrax and the elephant easily fall into a natural grouping.

The finer structure of the elephant's placenta is badly in need of further study. However, from the studies of Turner (1876), Assheton and Stevens (1905), Assheton (1906), and Boecker (1907), it is accepted as being deciduate. From the poorly illustrated and rather incomplete account of Boecker it appears likely, moreover, that the intricate placental labyrinth is hemochorial. Grosser (1927) accepts it as being hemochorial. This evidence regarding its microscopic nature, scanty as it is, lends some additional support to my thesis of the similarity between the placenta of the manatee, Hyrax and the elephant. It seems most likely for the present that the closest affinities of the elephant's placenta are to the type of zonary, deciduate, hemochorial placentation which characterizes both the manatee and Hyrax.

In view of the present observations upon the manatee and the suggested close affinities of the Hyracoidea, Proboscidea and Sirenia in regard to placentation, I have undertaken a revision of a diagram used in a previous paper to illustrate graphically the types of placentation occurring in mammals (text-fig. 2). The diagram is borrowed for this purpose from one originally presented

by W. K. Gregory (1910) to show his concept of the relationships of the orders of mammals.

The solid disks represent the monotremes and marsupials. The broken circles represent the orders of mammals in which the trophoblast exhibits little or no invasive tendencies, hence placentation in these has been termed diffuse



Text-fig. 2. The author's schematic representation of the types of placentation in mammals, revised in accordance with the considerations derived from the present study. The original diagram is borrowed from the work of W. K. Gregory (1910) representing his conception of the probable relationships of the orders of mammals. For a discussion of the diagram see text.

or adeciduate (epitheliochorial or partially syndesmochorial). The lemurs, Cetacea, Artiodactyla, Perissodactyla and Manidae constitute this class. The unbroken circles represent categories of mammals in which the trophoblast is extensively invasive, hence placentation is deciduate (endotheliochorial and hemochorial types). The endotheliochorial type of placentation is represented by the carnivores and Bradypodidae. The remaining large bulk of mammals possess so-called hemochorial placentae. Hemochorial placentation in the sundry groups of mammals shows a considerable morphological diversification indicating that it has followed several evolutionary paths from the primitive

type or types from which it arose. The marked similarity of placentation in the Hyracoidea, Proboscidea and Sirenia indicates that we are dealing in these orders of mammals with a well-defined placental type which differs in many outstanding ways from other hemochorial types. The similarity in the mode of placentation in these three orders coincides well with the generally accepted view that they are in other respects fairly closely allied. The Hyracoidea, doubtlessly the most primitive of the three, are thought by some to bear resemblances, on the other hand, to a primitive proto-ungulate stock. How the ungulates derived their diffuse placentation on the one hand, and the Hyracoidea, Proboscidea and Sirenia their hemochorial placentation on the other hand, must remain open for further study to attempt to elucidate.

SUMMARY

An excellently preserved fetus (44 cm. from snout to tip of tail) of the Florida manatee (*Trichechus latirostris*) in situ with membranes and placenta forms the basis of the present account. The only other descriptions of placentation in the Sirenia are by Harting (1878) and Turner (1889) on two rather inadequately preserved specimens of *Halicore dugong* (fetuses 28 and 163 cm.). Their histological examinations were necessarily brief. According to them, the placenta is at first diffuse, later zonary, while limited microscopic examination shows it to be non-deciduate with simple interlocking of intact endometrial and chorionic villi.

In the present specimen the membranes and placenta occupy solely the right uterine cornu. The placenta is zonary and sharply delimited. The allantois is voluminous filling the chorion from pole to pole, leaving only a small triangular area for amniochorionic fusion. The allantois is subdivided into four large compartments which communicate between the pedicles of four leashes of blood vessels constituting the umbilical cord. Thus the allantoic vessels form the septal margins of the four allantoic sacculations. There is no yolk sac at this stage.

The placenta on microscopic examination is found to be composed in its entirety of intimately fused chorionic and uterine tissues, producing a fine-meshed labyrinth of a hemochorial, deciduate variety. There is provision for histiotrophic nourishment of the fetus through the formation at the fetal surface of the labyrinth of lacunae containing stagnant maternal blood which is phagocytized by specialized trophoblastic cells.

The membranous chorion is covered by palisade-like, columnar cells. The endometrium outside the site of the zonary placenta at this stage is fully clothed by epithelial cells. The uterine glands are not very conspicuous, playing no great rôle in placentation. The allantoic sac has over the placental area numerous mesenchymal appendages protruding into it; the amnion is provided with extremely minute carunculae.

The organization of the placenta of *Trichechus latirostris* places this animal in the ranks of the Deciduata with a placenta of the hemochorial type, and removes it in regard to placentation from any close association with the Cetacea, Artiodactyla, or Perissodactyla. From various considerations it appears to be most closely allied in regard to placentation to the Hyracoidea and Proboscidea. Accounts of the placenta of the latter forms describe them as being zonary and hemochorial and hence distinctly unlike the endotheliochorial placentae of carnivores which they resemble only in regard to outer form. The evidence adduced from the present study supports the conclusion that placentation in the manatee, Hyrax and the elephant is of a closely related and distinctive hemochorial type.

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EXPLANATION OF THE PLATES

ABBREVIATIONS USED IN PLATES 1 AND 2

Acc. pl.	Accessory placental areolae
All.	Allantois
All. c.	Allantoic cavity
All. app.	Appendages in wall of allantois
Am.	Amnion
Am. c.	Amniotic cavity
Am. ch.	Amniochorion
Art.	Artery
Bl.	Urinary bladder
Cer.	Cervix
Ch.	Chorion
Corp. ut.	Corpus uteri
Memb. ch.	Membranous chorion
Mes. 1 and 2.	Cut mesenteries of reduplicated allantoic membrane
Pla.	Placenta
Umb. v.	Umbilical vessels
Ureth.	Urethra
Vag.	Vagina
Vor.	Vortex

PLATE 1

PLATE 1

Fig. 1. Semidiagrammatic representation of the pregnant uterus, placenta and fetal membranes of the manatee. x $\frac{3}{8}$. The placenta is zonary. The allantoic sac completely surrounds the amnion leaving only a small triangular field where the amnion is in apposition to the chorion. At the apex of this triangle there is a vortex-like indentation on the placental surface. The umbilical cord divides into four leashes of blood-vessels which attach to the placenta. In addition to these there is a smaller, single artery which follows a circuitous route to the opposite side of the placenta.

The uterus is bicornuate, the fetus occupying the right cornu solely. The two cornua unite in forming a short corpus uteri which terminates in a well-defined cervix.

Fig. 1, a. This sketch shows the appearance of the cervix and vagina, as well as their relationship to the urethra. x $\frac{3}{8}$.

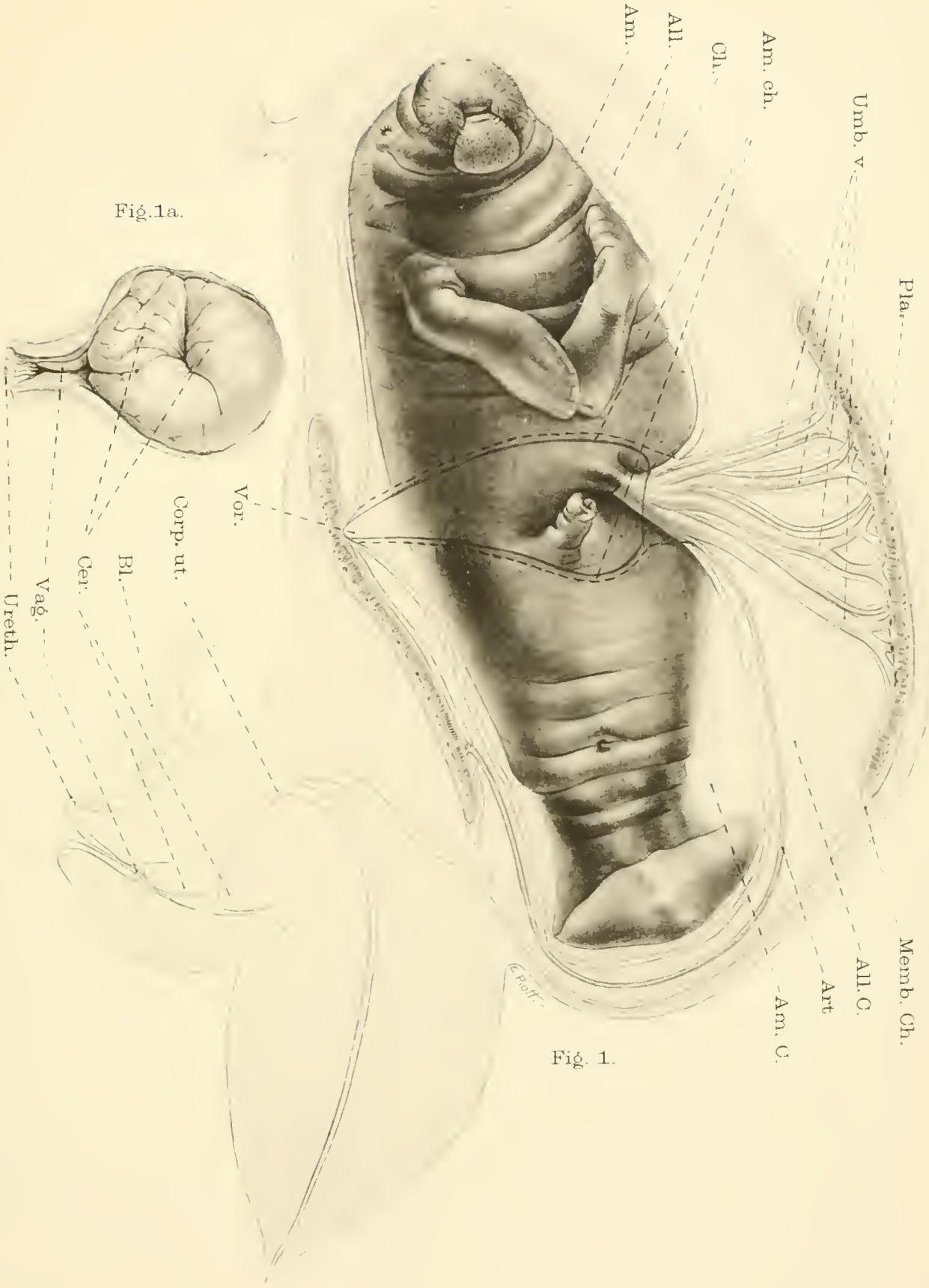


Fig. 1.

Fig. 1a.

THE HELIOTYPE CORP. BOSTON

PLATE 2

PLATE 2

Fig. 2. Semidiagrammatic drawing of the placenta and fetal membranes of the manatee. x $1\frac{3}{0}$. The zonary placenta is shown unrolled exposing the allantoic and amniotic sacs. The amnion is shown as an oval sac with its wall partly removed. The allantois surrounds the amnion completely excepting a small triangular area where the amnion fuses with the chorion on the surface of the placenta. The allantoic sac consists of four compartments, — two smaller ones (indicated by arrows extending into them) which lie against the placental surface; and two larger ones extending around the amnion and to the poles of the chorion, the outlines of which cannot be so definitely shown because the whole specimen has been cut open and flattened out. The four pedicles of the umbilical cord are shown. They are clothed by allantois and possess mesenteries derived from the allantois. Between pedicles I and III the entrance into one of the lesser allantoic compartments is seen; between pedicles III and IV the communication into the second of the lesser compartments is seen. Pedicle II is attached by its allantoic mesentery to the wall facing the observer, so that the mesentery is shown as having been cut (Mes. 1). When the specimen is considered as having been folded up in its natural position with the girdle of the placenta restored, this mesentery attaches to the amnion. The points marked Mes. 1 and Mes. 2 on opposite sides of the drawing then become attached to one another. The depression or vortex where the amnion and apices of the two lesser allantoic compartments meet is shown. The appendages on the walls of the placental vessels are indicated. Also several dark spots are shown near the left border of the placenta; these are the minute accessory placental areolae. The entire chorion is well vascularized. The small artery (Art.) arising from the root of pedicle IV of the umbilical cord is shown coursing around the circumference of the amnion to reach the opposite side of the placenta.

Fig. 2

PLATE 3

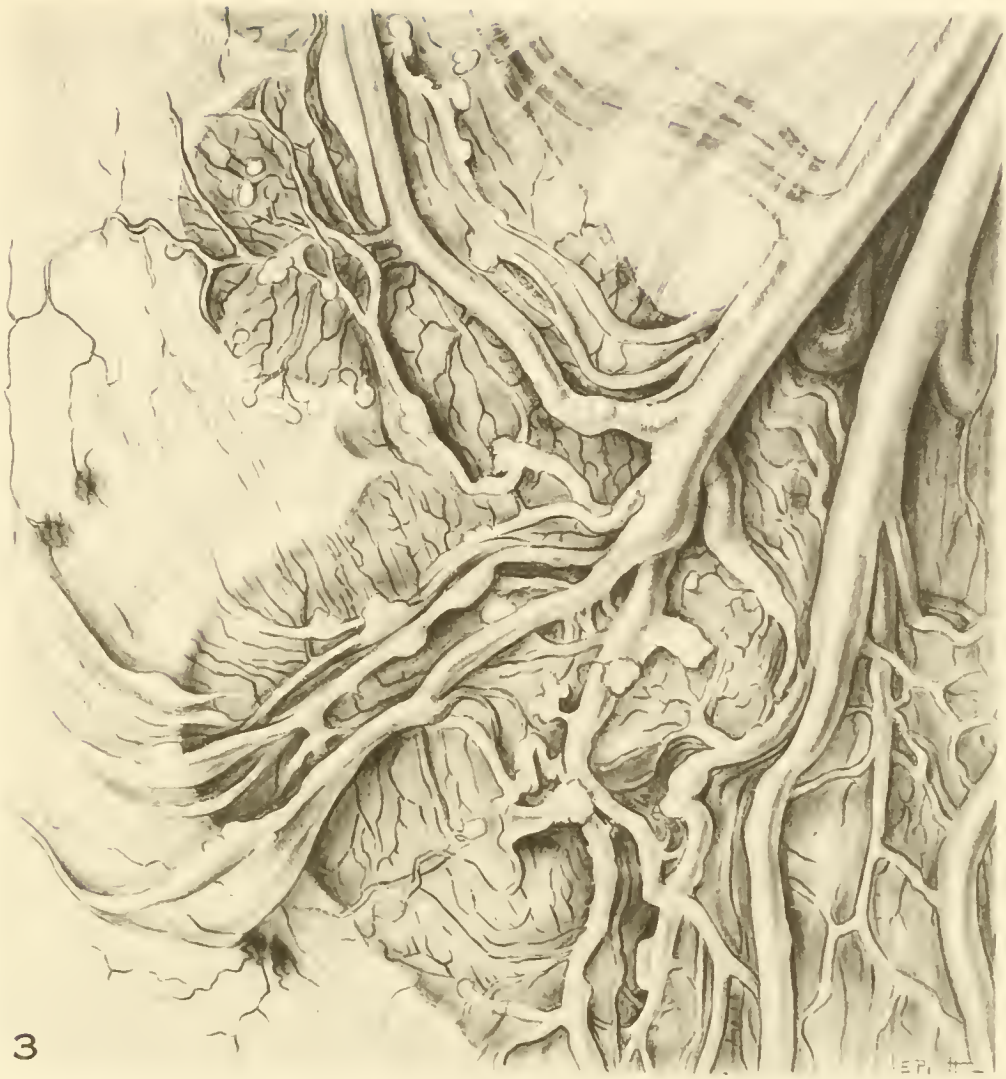
PLATE 3

Fig. 3. A drawing showing the detailed character of the surface of the placenta. The illustration shows the finer ramifications of the blood vessels of the umbilical pedicles III and IV upon the surface of the placenta. The appendages upon the walls of these vessels are seen protruding as bulbous projections into the allantois. At the top of the figure on the right a mesentery of the allantois is shown enfolding the umbilical pedicle. The deep fissure between the two diverging umbilical pedicles is the entrance to one of the lesser allantoic sacs. On the left border two small, dark, round patches are accessory placental areolae. x $\frac{4}{5}$.

Fig. 4. Detailed sketches of the walls of placental vessels showing their variable and peculiar appendages. x 1.

Fig. 5. Sketch of a free-hand section made through the placenta and the wall of the uterus. The placental labyrinth is dark owing to the presence of blood. Beneath the labyrinth is a lamina of uterine tissue containing macroscopically visible maternal blood vessels. x 1.

Fig. 6. Sketch of several accessory placental areolae seen attached to the membranous chorion after pulling them loose from the uterus. x 1.



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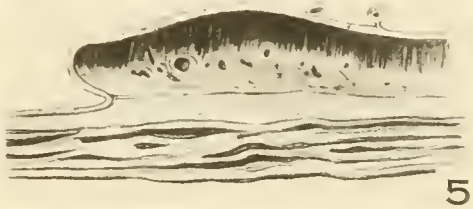

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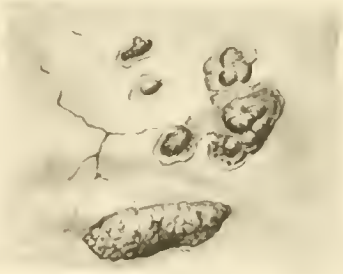

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PLATE 4

PLATE 4

Fig. 7. A section through the placenta showing the dark-staining placental labyrinth resting upon a more lightly stained lamina of uterine tissue. x 9.

Fig. 8. The placental margin showing the placenta to the right, and the membranous chorion, uterine cavity and uterine mucosa to the left. x 9.

Fig. 9. Cross-section of the umbilical cord, taken about 2 cm. from the body-wall. There are two umbilical arteries, one vein and an extensive cleft, the allantoic duct. x 6.

Fig. 10. An accessory placental areola, with edges somewhat torn, showing, however, that these minute areas have the same structure as the placenta itself. Note the cushion of proliferated endometrium upon which the placental labyrinth rests. This cushion ceases at the edges of the areola where uterine mucosa fully covered by epithelium begins. Notice in this low-power picture, which comprises the whole thickness of the mucosa, how infrequent and small the uterine glands are. There are a few scattered here and there almost at the limit of visibility. x 9.

Fig. 11. The uterine mucosa, a few centimeters from the placental border, showing the presence of intact, columnar epithelium. In the center of the photograph there is a structure, quite frequently encountered in the sections of the uterus, which is interpreted as being a minute cyst of the epithelium. x 125.

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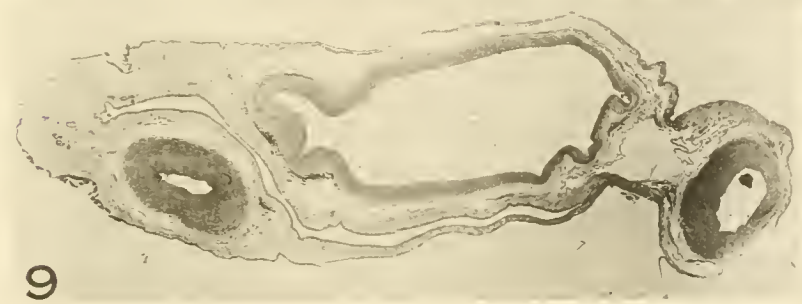

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THE HELIOTYPE CORP. BOSTON.

PLATE 5

PLATE 5

Figs. 12, 13, 14, 15 and 16 should be examined in the order named. They represent sections taken at succeeding levels from surface to base of the placental labyrinth. Fig. 12 is from the labyrinth at the surface of the placenta, with closing plate of fetal mesoderm at the top. The curious arcades of trophoblast can be seen enclosing spaces into which stagnated maternal blood escapes. The trophoblast enclosing these spaces is differentiated into columnar cells which are actively phagocytic, being filled with phagocytized red blood cells and pigment. x 250. Fig. 13. Slightly below the previous section showing the character of the outer third of the labyrinth. It is characterized by fine-meshed trabeculae of trophoblast separating the fetal from the maternal blood-streams. x 250. Fig. 14. At a deeper level showing the character of the middle and most of the inner third of the labyrinth almost down to the base of the placenta. This fraction of the labyrinth is composed of a fine-meshed network of trophoblast in which trabeculation is not so obvious. x 250. Fig. 15. The base of the placental labyrinth showing the tongues of fetal mesoderm covered by trophoblast which penetrate into the uterine mucosa. x 125. Fig. 16. The uterine glands are not numerous or large, and tend to occur scattered in little clusters as illustrated here. x 125.

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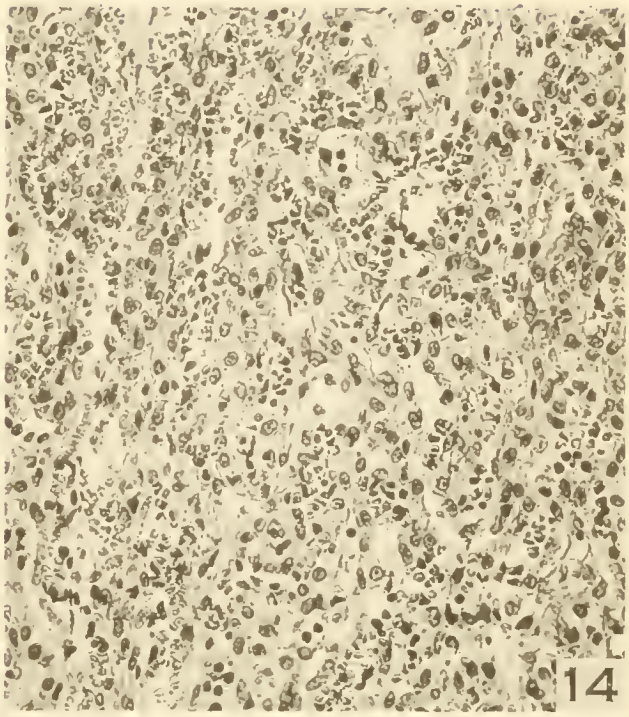
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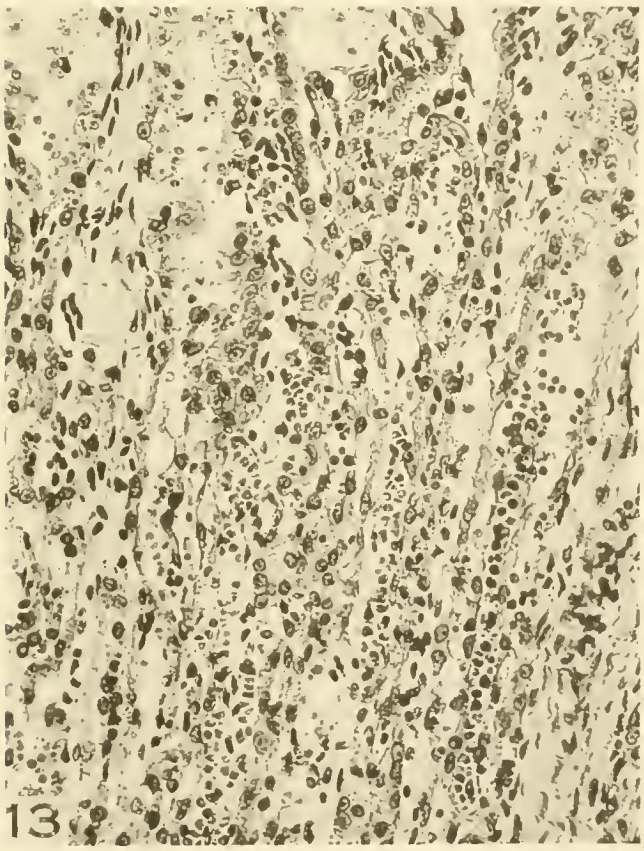
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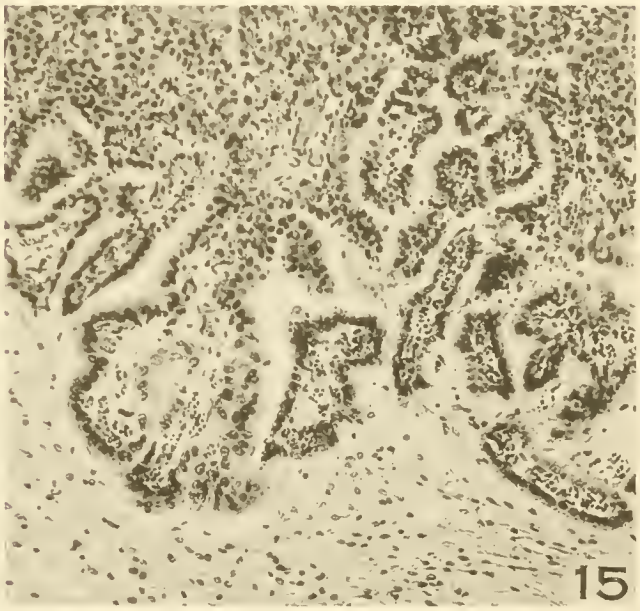
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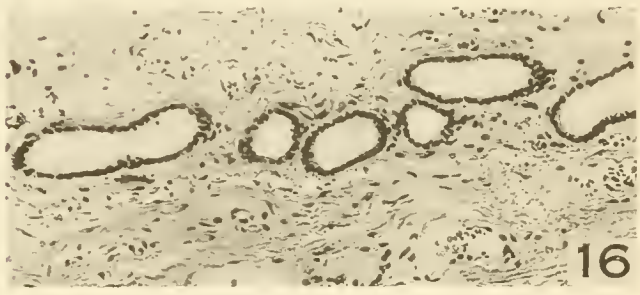
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PLATE 6

PLATE 6

Fig. 17. The trophoblast and fetal mesoderm at the base of the placenta sending out tongue-like processes which are pushing their way along the walls of a maternal blood vessel. Endothelial cells can be seen lining the vessel. x 125.

Fig. 18. Two maternal vessels in cross-section showing cuffs of fetal tissue surrounding them. In the uppermost vessel one can see remnants of the flattened maternal endothelium. Next follows a zone of pale-staining syncytial trophoblast; then a layer of fetal mesoderm containing fetal capillaries; thereupon a festooned layer of cytotrophoblast which exhibits deep nuclear staining; and finally the large fields on all sides of uterine connective tissue. x 125.

Fig. 19. Section through the wall of a large, maternal vessel filled with blood corpuscles. The trophoblast has surrounded this vessel creating a double layer of trophoblast with a lamina of fetal connective tissue and blood capillaries in between. The inner and outer layers of trophoblast are quite distinctive in appearance. x 120.

Fig. 20. A dilated uterine gland containing secretion — an uncommon finding — into which a tongue of fetal tissue has erupted. x 120.

Fig. 21. A maternal vessel half surrounded by fetal tissue to illustrate the actual continuity of the inner and outer layers of trophoblast. The trophoblast which erodes the wall of and flattens out against the sides of the maternal vessel becomes markedly altered in character. x 120.

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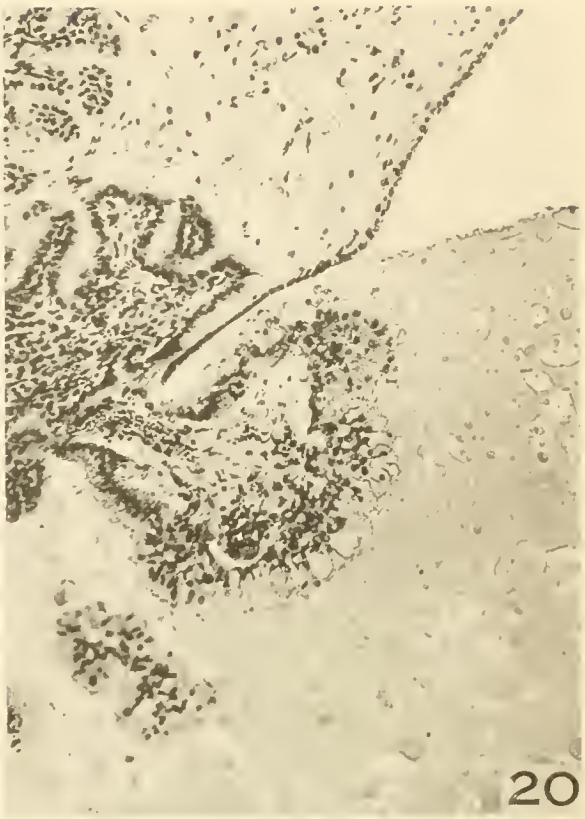
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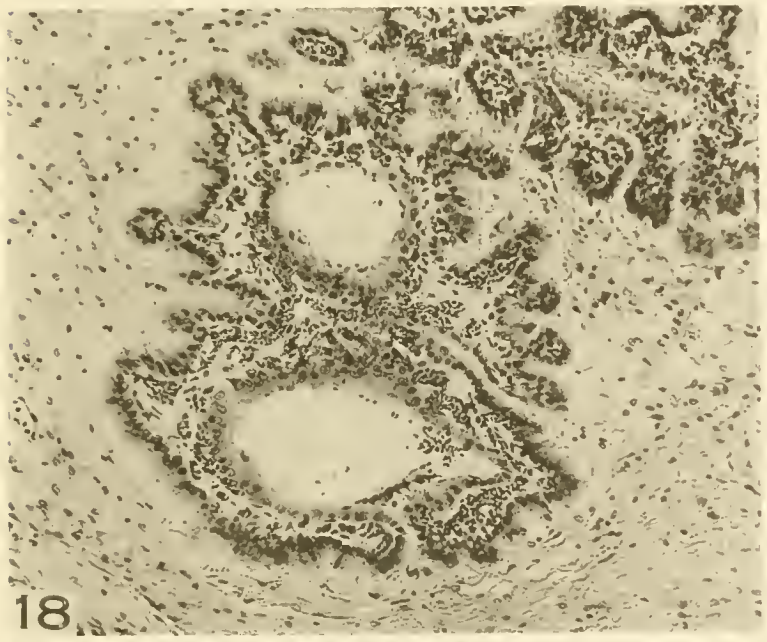
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PLATE 7

PLATE 7

Fig. 22. The surface of the placental labyrinth to show the curious spaces lined by trophoblast which contain escaped maternal red blood cells. To the left two such spaces where the trophoblast is actively phagocytic; to the right a space different in appearance which is an afferent maternal blood vessel lined by endothelium and surrounded by trophoblast. It is from vessels of this type that blood escapes into the neighboring lacunae as well as into the meshes of the placental labyrinth. x 125.

Fig. 23. A maternal vessel at the fetal surface, not far from the margin of the placenta. The blood lacunae which contain escaped maternal blood and which are interposed between the large vessel and the fetal closing plate, are small here. In the lower half of the picture the labyrinth which is fed by the large vessel is visible. x 120.

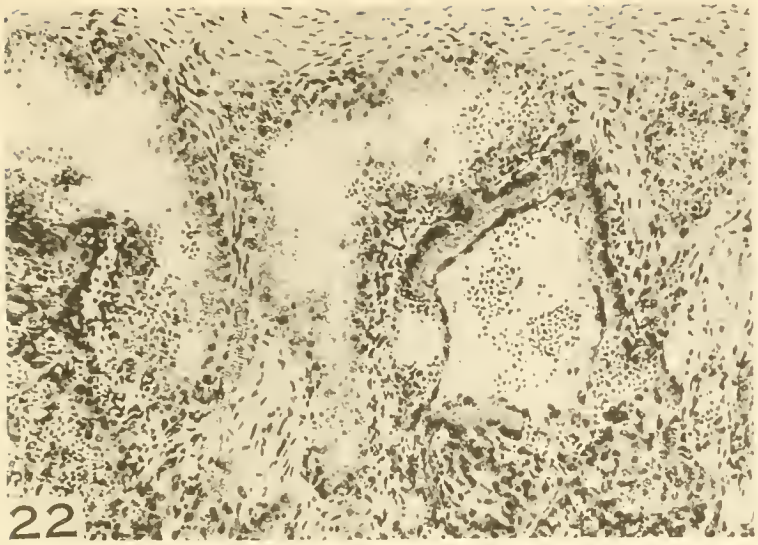
Fig. 24. The membranous chorion, showing the chorionic epithelium on the left and the allantoic epithelium on the right. x 125.

Fig. 25. An appendage of the allantois on the wall of one of the placental blood vessels. Note that these structures are composed of a loose, mesenchymal tissue. x 9.

Fig. 26. The stroma of the foregoing appendage shown more highly magnified. x 125.

Fig. 27. The allantoic epithelium composed in places of such club-shaped cells with vacuolated distal ends. x 320.

Fig. 28. The amniotic epithelium highly magnified to show the minute excrescences composed of stroma and modified epithelial cells by which its surface is covered. x 320.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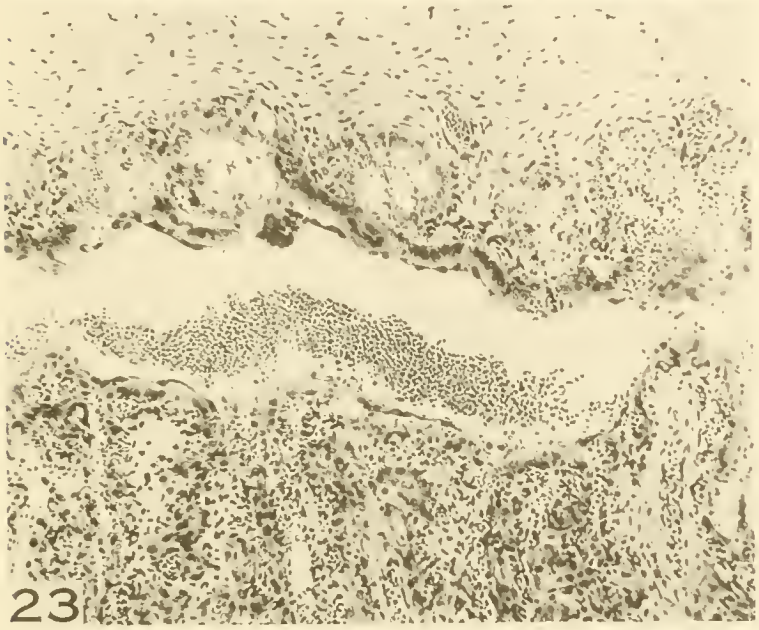
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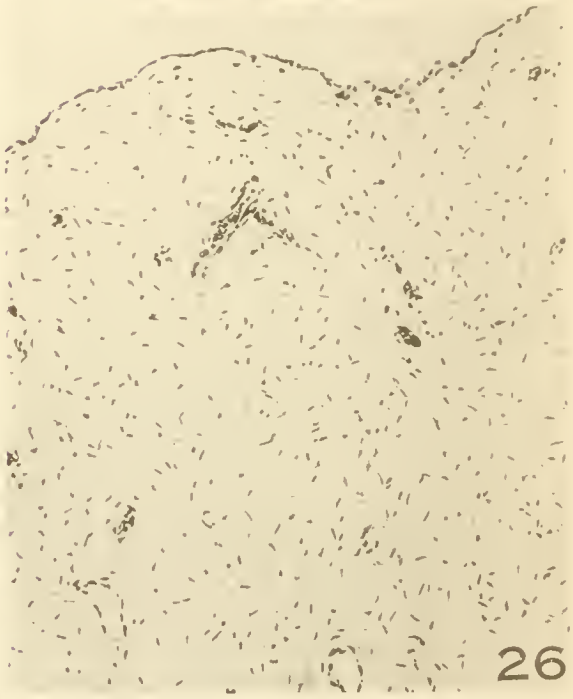
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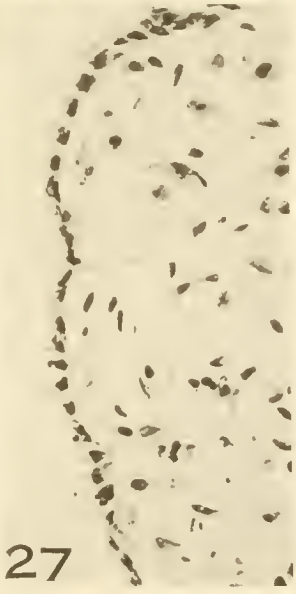
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